5.—Homing Behaviour in the Quokka, Setonix brachyurus (Quoy and Gaimard) (Marsupialia)

By W. C. Packer*

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Quokkas collected in the settlement area of Rottnest Island exhibit homing behaviour following translocation over distances of up to 1.75 miles, the maximum distance tested. Within familiar territory they are able to orient themselves rapidly and behave appropriately in relation to the physical character of the habitat but behave inappropriately in unknown areas. It is not clear, however, whether homing involves true orientation and navigation or a random-search technique. The area within the settlement in which any individual animal was recaptured was extremely variable in size but in most cases probably did not represent the complete home range.

Introduction

Dunnet (1962) and other investigators (unpublished data) suggest that the quokka (*Setonix brachyurus*) is generally rather restricted in its movements, although this may vary considerably from population to population. Dunnet found that the animals have relatively restricted individual ranges on the eastern end of Rottnest Island but have been recaptured over distances of up to 2,000 yards from the original site of marking. He suggests, however, that those on the western end of the island are more restricted in their range (no more than 300 yards on the basis of limited data).

Following from these observations, the question arose as to whether or not the quokka possessed the ability to return to its home area if translocated from it. Associated with this is the question of the size of the individual ranges.

Methods and Materials

Rottnest Island, 12 miles west of Perth, Western Australia, supports a large population of quokkas. There is a tourist resort at the eastern end of the island, and with the exception of one series (see below) all of the animals were taken from this settlement area. Although not typical quokka habitat in any sense, this area was chosen because the animals there are accustomed to people and can be approached closely. This allowed one to identify marked animals without the need for physically handling them subsequent to marking.

Each animal was marked in two ways. They were fitted with plastic collars which bore individually recognizable symbols of reflective tape (see Ealey and Dunnet 1956) which were easily distinguishable with the naked eye at distances of 10 to 20 feet. A numbered operculum tag (see Dunnet 1956) covered with red reflection tape, was fastened to the pinna of one ear. This greatly reduced the time spent in locating marked animals since this marker was easily visible in the beam of a head-torch up to 100 feet and stood out clearly when the animal was facing directly toward or away from the observer at which times the collar was obscured.

In January and February, 1961 (mid-summer) four series of animals were collected in the southern end of the settlement and marked. The release points for these series, Bungalow No. 1 at the northern most end of the settlement, Herschell Lake, Lake Bagdad and Parakeet Swamp, are shown in Figure 1 and numbered, respectively 1 to 4. At the same time two additional series were marked but not translocated. One of these came from the southern end of the settlement and served as the control and the other was captured at the fresh-water soak on the north shore of Herschell Lake.

The settlement area was searched for marked animals about three times a week for six weeks and then at irregular intervals until the middle of May. All recaptures were visual sightings only, and all were recorded in order to obtain a measure of the individual ranges.

During January and February, environmental conditions are quite severe for the quokka. Over most of the island, fresh water is available only from soaks along the edges of the lakes. The lakes themselves are highly saline with a chlorinity of approximately 70 parts per thousand in Bagdad and Herschell (Hodgkin 1959).

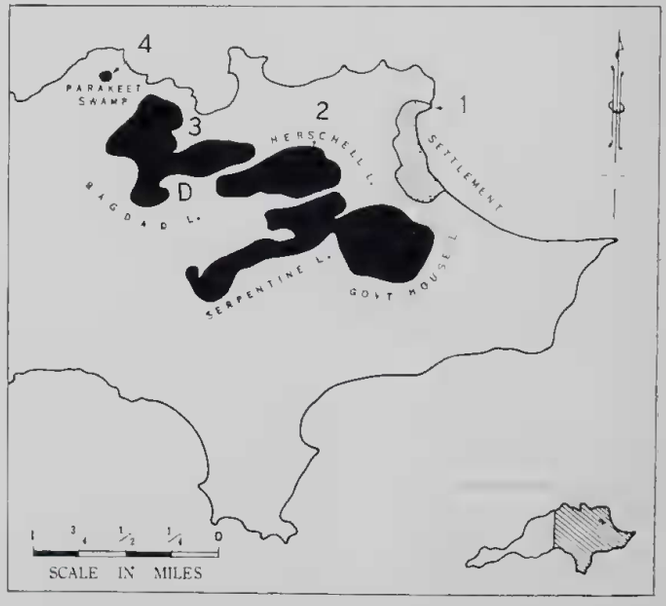

Fig. 1.—Map of eastern half of Rottnest Island, Western Australia, showing release points (1-4) of translocated quokkas.

* Zoology Department, University of Western Australia, Nedlands, Western Australia.

Most of the vegetation is dry also. The settlement area at this time is an "oasis" where leaking taps and friendly tourists keep the animals supplied with water and food. As a result, the animals here are never as poor physiologically as their "non-civilized" cousins (unpublished data).

In the event that the settlement was an exceptionally attractive area during the summer, so producing atypical homing results, a small series of animals was translocated from the settlement to the Lake Bagdad site in August, 1961 (mid-winter). At this time of the year fresh water is widely available, the vegetation is green and tourists are few. The control series consisted of animals marked the previous summer and seen in the settlement on the two evenings when the translocated series was collected. Because of other commitments on the mainland, the settlement was searched for marked animals only at irregular intervals over the next two months.

Results

The number of animals marked in each series and the number and per cent. recaptured one or more times in the settlement area are shown in Table I. The per cent. of summer animals returning to the settlement decreased as distance of translocation increased, but there is no significant difference between the three closest points on the basis of a chi-square test. A significant decrease in the number making the return is found, however, in the group released at Parakeet Swamp when compared to the other sites (χ^2 13.74, 1.d.f.). The proportion of the settlement control animals recaptured is somewhat greater than that of translocated animals from the three closest points but is not significantly different ($\chi^2 = 2.87$, 1.d.f.).

When the work was partially repeated during the winter the number of the translocated animals returning from the Bagdad site was significantly less than during the summer ($\chi^2 = 3.95$, 1.d.f.). While the control series was small, the results are comparable with the summer controls.

The non-translocated series marked at Herschell Lake requires special comment. These animals represent a nearby but relatively distinct population of quokka. Only one of this series was ever seen in the settlement. Prior to this recapture this individual was observed in an intermediate location between Herschell Lake and the settlement but was never recaptured subsequently. Of the other 19 animals in the series, 12 were never recaptured except along the soak at which they had been collected originally; two were recaptured at Herschell and on the golf course which in part separates the lake from the settlement; and two were recaptured only on the golf course. Three were never recaptured.

TABLE I

Number of quokkas marked and recaptured and distance translocated.

Series	Distance from capture site	Number marked	Recapture 1 or more times in settlement	
			No.	%
Summer				
Bungalow I	0·33 mile	14	12	85·7
Herschell L. ..	0·67 mile	23	19	82·6
L. Bagdad	1·25 mile	25	19	76·0
Parakeet Swamp	1·75 mile	25	10	40·0
Settlement controls .		32	30	93·8
Herschell controls	...	20	1	5·0
Winter				
L. Bagdad	1·25 mile	21	10	47·6
Controls ..	..	10	9	90·0

The release points for the translocated series were checked on the two nights following release and at irregular intervals after that. No marked animals were seen except on the first night. Traverses by road over the north-east corner of the island were made as often as possible, but no marked animals were seen except at the rubbish dump (point D on Fig. 1) which at that time supported a large population of quokkas. These included one from Herschell, two from Bagdad and four from Parakeet. These animals were not seen on every occasion, but they were never recaptured subsequently in the settlement or elsewhere.

There was no significant difference between the sexes in the translocated series as to whether they homed or not ($\chi^2 = 0.85$, 1 d.f.), and there is no evidence to suggest that age was a factor either, although no animals less than 18-20 months old were tested.

The number of animals returning from Bagdad during the winter was significantly less than in the summer ($\chi^2 = 3.95$, with 1 d.f.), but whether this is because of more favourable environmental conditions during the winter is not clear. Except for the few summer animals that apparently established new ranges around the rubbish dump, none of the translocated animals who failed to return to the settlement were seen. It is not known whether they set up new ranges elsewhere or if they even survived.

A total of 419 recaptures of marked animals was made, comprising 176 of controls and 243 of translocated animals. The frequency of recapture ranged between 1 and 14 with a medium of 5.4. Although the area in which any one animal was recaptured probably does not represent its home range (see Discussion), nevertheless, certain measurements can be made utilizing the locations of recapture, i.e., area and proximity to marking site of subsequent recapture.

Area:—The site of original capture and of all recaptures for each animal was plotted, and the area enclosed within a polygon, formed by connecting the most peripheral of these points, was calculated. The size of the area thus obtained was extremely variable and ranged from approximately 3,900 to 178,000 square feet with a median of 26,300 square feet. The values were not normally distributed about the mean (*c.*41,700 square feet) but were skewed toward the low side. The relationship between area and number of recaptures was also extremely variable and ranged from 10 recaptures within an area of 5,400 square feet to three recaptures within 151,500 square feet, The minimum number of

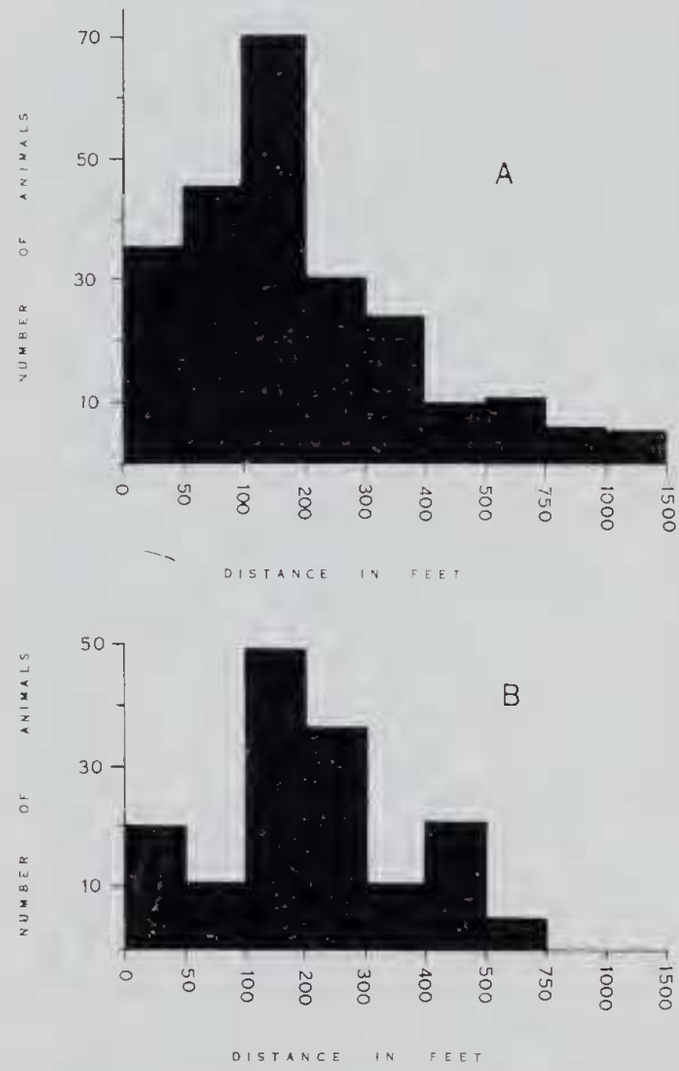

Fig. 2.—Distance of all recaptures from the site of marking of (A) summer translocated animals and (B) non-translocated summer animals; grouped for various distance classes.

recaptures required to establish the size of the range could not be determined from the data.

Proximity of recapture:—No true measure can be made of the precision of the return because of a lack of knowledge of the nature of the home range and of how to interpret the position of the original capture site. Nevertheless, it is interesting to note how close subsequent recaptures were made to the point of marking.

Figure 2 shows the frequency distribution of the distance between the site of original marking and all subsequent recaptures for the (A) summer translocated animals and (B) settlement controls. The distances are grouped within classes of varying magnitude. The shape of these curves varies somewhat with significantly more of the recaptures of the translocated series being made within 100 feet of the marking site than is the case with the non-translocated individuals ($\chi^2 = 5.17$, 1 d.f.). In both cases, however, the mode of the distribution is between 100 and 200 feet. The same mode is obtained when each of the four translocated series is plotted separately.

Figure 3 shows the frequencies of recapture at various distances for the first and for the closest recapture. The distribution of the distances of first recapture (Fig. 3 A and C) are somewhat different from each other, while those for the closest point (Fig. 3 B and D) are generally comparable. The reason for the greater disparity in the two graphs for the translocated animals can be traced to the fact that in almost one-half the cases (27 out of 60) the animals moved closer to the marking site subsequent to the first recapture. Only one-third (10 out of 30) of the controls made a comparable move. However, the first recapture point in control animals was generally closer to the marking site than with the translocated animals. Even so, the number of non-translocated animals first recaptured within 100 feet of the marking site was not significantly greater than among the translocated animals ($\chi^2 = 0.90$, 1 d.f.).

One further comparison is worthy of note. The area in which the winter controls were recaptured overlapped the area in which these same animals were found during the summer in eight of the nine cases; and in the one which did not overlap, the two areas were separated only by about 100 feet. This would suggest that there is no change in location, at least in this portion of the home range, between summer and winter. The winter areas were

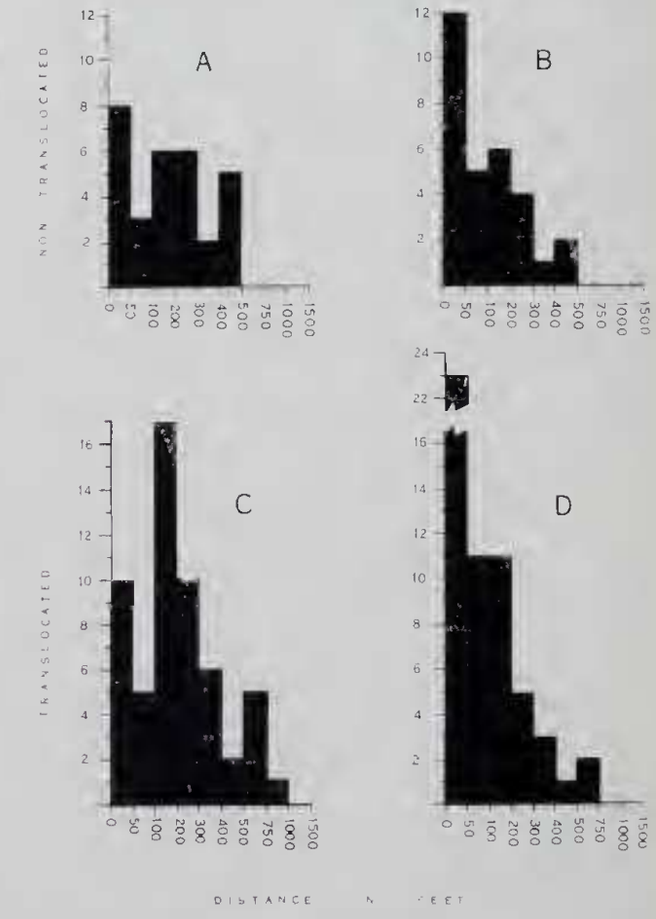

Fig. 3.—Frequency distribution of the distance between the site of marking and the 1st recapture point (A & C) and the closest recapture point (B & D) for translocated and non-translocated animals in the summer.

generally small, but this may have been a function of fewer recaptures over a shorter period of time.

Discussion

These results clearly demonstrate the existence of homing behaviour in the quokka. Whether this is achieved through true orientation and navigation or by some random-search technique is not known. Regardless, it must be extremely efficient judging not only by the per cent. of recovery but also by the speed with which it is performed. Among the animals translocated to Bungalow No. 1 and to Herschell Lake, one from each series had returned within 24 hours. By the fifth night after release twelve had returned from Herschell and animals translocated to Bagdad during the summer were recaptured three days after release. No accurate measure can be made for return from Parakeet Swamp or from Bagdad during the winter because it was not possible to continue the survey daily; however, five animals from Parakeet (one-half the total) were recaptured the eleventh night after release and four from Bagdad (almost one-half) were recaptured on the sixth night after release.

The possibility that some of the animals may have visited the release point in the course of excursions away from the settlement cannot be disregarded. On the basis of Dunnet's (1962) observations, animals from the southern part of the settlement could range as far as the two closest release points. All that can be said here on this point is that no control animal from the settlement was ever seen at either of these two points, and only one animal marked at Herschell Lake was ever seen in the settlement. It is unfortunate that this latter individual was never recaptured again.

Although homing in this species may not involve navigation, a series of unplanned observations in the course of this work clearly suggests that the quokka is able to orient itself rapidly within its home area and to respond appropriately. The fresh water soak at which animals were collected for the non-translocated series at Herschell runs for about 200 yards along the edge of the lake. During the summer the level of the lake is reduced, and the shore is 20 to 50 feet wide. Behind this rises a wall of Pleistocene dune limestone which shows a bench and notch configuration resulting from fluctuation of sea-level during geologically recent times; this is figured by Teichert (1950) for one of the other lakes. The animals move freely over this cliff on pathways.

The animals in this non-translocated series were collected, placed in bags, taken to the settlement, marked and then returned to the shore of the lake and released. Upon release most of them appeared to be in an excited state and rapidly moved off up or down the beach or up the cliff-face. On the other hand, some of the translocated animals released at Herschell, although handled in the same way, responded quite differently. When released on the shore, they too moved off rapidly; but if they happened to be heading toward the water, they just kept going, regardless. They could be followed in the water in the beam of a head-torch for at least 100 feet. This behaviour was never observed in the control series; and the quokka has never been observed to enter the salt lakes except very rarely when chased by man, although they frequently wade in one or two inches of water around the edges of the fresh-water swamps during the winter. The morning following release, three dead animals (not included in Table I) were found washed up on the shore.

Arising from these observations, an attempt was made to see if the quokka could and would orient within a restricted area. For this purpose an octagonal enclosure 150 feet in diameter was built. The terrain was such that the only visible landmark was the lighthouse which is situated on the highest point in the centre of the island. Single animals were released by remote control in the centre of the area and were captured in traps situated at the eight angles. All tests were run on clear, moonless nights and involved animals captured in different directions from the enclosure and at various distances up to two miles. As can be seen in Figure 4a, the animals were captured at random around the enclosure in relation to the home direction. In a series of preliminary experiments, the animals responded negatively in relation to the observer, but after modification of the apparatus this no longer occurred (Figure 4b).

Although the number of animals tested was relatively small, there is nothing to suggest that under the conditions of the experiment additional animals would have changed the results. Animals taken from one-quarter mile away were no better in their orientation that those from the settlement two miles away. This is somewhat unexpected, since the near-by individuals were from an area from which animals are known to move to the site of the enclosure. Those animals might be expected to be familiar with the area and, therefore, to return to the home area by the most direct route. While these results do not support an hypothesis involving true orientation and navigation as a factor in homing, it is probably too early to say that the mechanism involves only random-search. Different techniques will be required to differentiate the two.

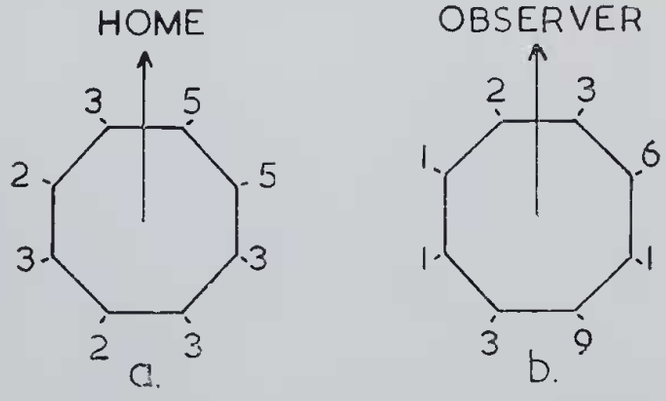

Fig. 4.—Position of recapture within an enclosure in relation to (a) the home area and (b) the observer.

An interpretation of the individual areas within the settlement in which recaptures were made is difficult to make. The method used in determining the size of these areas was essentially the minimum area method used by several authors (reviewed by Brown, 1962), although in the present work the points represent visual sightings, not trap captures; and, therefore, the matter of boundary strips does not arise.

The area certainly does not correspond to the home range, at least as that term is applied by Burt (1943). Many of the smaller areas, particularly those in which ten or more recaptures were made, are open, grassy plots providing no diurnal shelter. In these cases the animals probably spend the day either in the near-by scrub or else under a building from which they emerge at night to occupy a small range in which they feed and possibly mate. On the basis of the present data, it is suggested that this is the general situation for this species. although the size of the area will vary with the individual. Excursions of various lengths with various frequencies may occur, perhaps influenced at the present site by the activities of tourists. A discussion of the relationship between excursions and the home range concept is beyond the scope of this paper.

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